THE WING-VENATION OF LEPIDOPTERA. (PRELIMINARY REPORT).

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(Seven Text-figs.)

This short paper is an outline of one portion of a paper upon which the author is engaged, to be entitled "The Panorpoid Complex: a critical study of the phylogeny and inter-relationships of the Holometabolous Insects, with special reference to the four Orders Mecoptera, Trichoptera, Lepidoptera, and Diptera." The genesis of the paper was the discovery of a remarkable large fossil insect, of a generalised type, from the Trias of Ipswich (Q.). In the structure of the wing-venation and wing-membrane of this insect, the writer recognises the nearest known approach to the true ancestor of these four Orders. The complete paper will be an attempt to show the diverging lines of descent of the four Orders from their common ancestor.

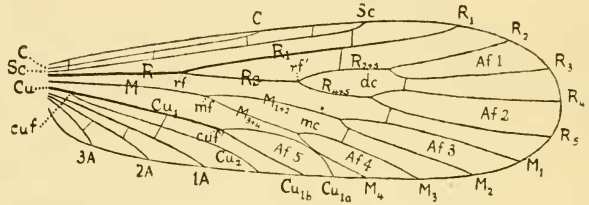
The fossil wing-form, which may be termed the *Protomecopterous* form, is exceedingly complicated, both in the actual venation, and in the structure of the membrane. The essentials of the type may be defined as follows:—

(i.) *Wing-membrane* with an abundant but *obsolescent* polygonal meshwork of small areolets or cellules, of Palæodictyopterous origin. Upon the angles of the areolets (and also upon the main veins), large hairs or bristles were developed. These are termed *macrotrichia*. Upon the whole wing-surface, much smaller and more abundant minute hairs, or *microtrichia*, are arranged.

(ii.) *Wing-venation* of Panorpid type, fore- and hindwings subequal. The essential characters of this venation are, (*a*) the

symmetrical dichotomous forkings of the main veins, Rs, M, and Cu_1; (*b*) the formation of large elongated polygonal (usually hexagonal) cells; (*c*) the formation of sessile apical forks upon the distal ends of the two principal cells (viz., the discoidal cell, *dc*, and the median cell, *mc*); and (*d*) the capture by Cu_{1a} of the fourth or last branch of the media (M_4).

Reduced to its essentials by the removal of numerous excess cross-veins and irregularities in the courses of the main veins, the Protomecopterous Venational Plan is shown in Text-fig.1 (forewing). For those readers who are not familiar with the



Text-fig.1.

Diagram of the Protomecopterous scheme of venation, with all excess cross-veins removed. Notice the partial fusion between Cu_{1a} and M_4. (In Mecoptera and Lepidoptera, this fusion becomes complete).

Comstock-Needham system of nomenclature, an explanation of the notation used is given at the end of this paper. The costal vein C is present in the Protomecoptera, but becomes entirely fused with the anterior border of the wing in the four descendant Orders (as, indeed, in all recent Insecta). The only differences between fore- and hindwings are :—

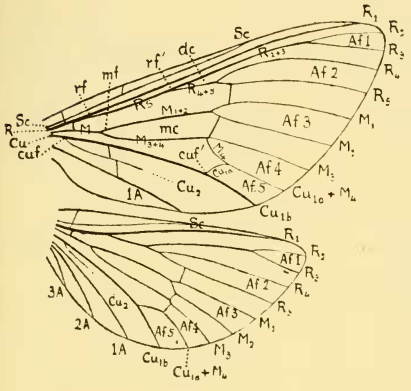
(*a*) Sc is reduced in length in hindwing.

(*b*) M tends to fuse basally with R in forewing, with Cu in hindwing.

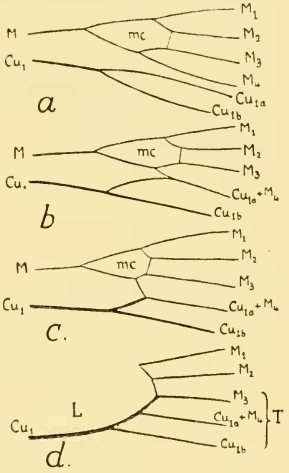
(*c*) Cu_1 (like Sc) is shorter in hindwing than in forewing.

The main object of this short outline is to indicate the interpretation of the Lepidopterous venational scheme as a *direct derivative* from the Protomecopterous Putting aside the *Micropterygidæ* (which will be dealt with as an archaic side-

branch derived by extreme reduction from the very base of the Lepidopterous stem, and having no near relatives within the Order as now existing), the author selects the *Hepialid* type of wing as the most archaic. Text-fig.2 shows the interpretation of the forewing of *Hepialus eximius* Scott.



Text-fig.2.*



Text-fig.3.†

In this wing, the capture of M_4 by the upwardly arching Cu_{1a} (which is not a mere cross-vein, as hitherto supposed, but a true branch of the main vein Cu_1) is beautifully shown. The possession of this character is *the essential basis for the production of the closed Lepidopterous cell.* After the capture of M_4 by Cu_{1a},

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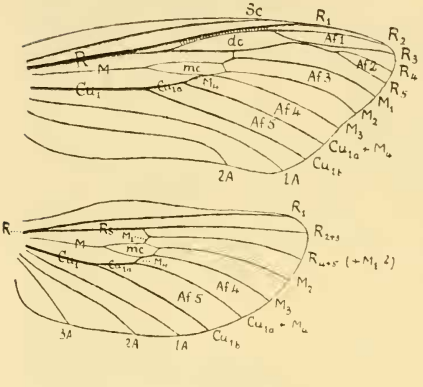
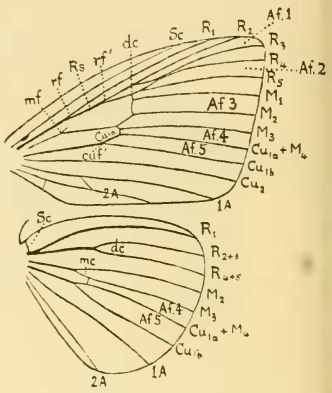
* Wing-venation of *Hepialus eximius* Scott. Note the close correspondence in venations in fore- and hindwings (homoneurism).

† Four phylogenetic stages in the formation of the *trigamma* (T)—*a*, primitive stage, with no fusion between Cu_{1a} and M_4; *b*, fusion between Cu_{1a} and M_4 completed (N.B., the wing in Text-fig.1 lies phylogenetically between *a* and *b*); *c*, beginning of alignment of the trigamma-stem; *d*, completion of the trigamma (T), with its strong stem and triple fork. (In *d*, the media, M, and its first dichotomy are omitted, as in most Lepidoptera).

near the base of the former, the small basal portion of M_4, left uncaptured, tends to become straightened out into line with the ascending base of Cu_{1a}. Thus there becomes formed a *strong three-pronged fork*, the *trigamma*, which forms the posterior closure of the Lepidopterous cell. The prongs of the trigamma are, from above downwards, M_3, $Cu_{1a} + M_4$, and Cu_{1b} respectively; and the method of its formation is indicated in Text-fig. 3.



Text-fig. 4.*



Text-fig. 5.†

The *trigamma* is the key which unlocks the homologies of all Lepidopterous wing-venational types. In Text-figs. 4-6, the author has applied it to *Zeuzera*, *Castnia*, and a butterfly, (*Euplœa*) representing three important and outstanding types of venation. In Text-fig. 7, the author has taken Hampson's "typical moth-venation" (p. 318 in Sharp's Insects, Vol. ii.), and, by slight alterations, has transformed it into a "typical moth-

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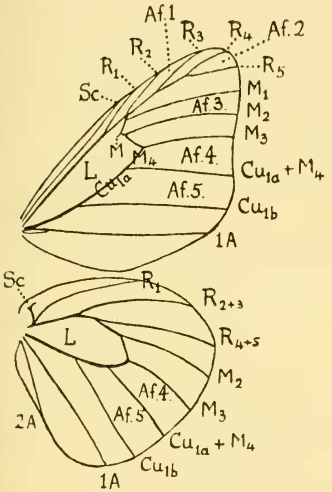
* Wing-venation of *Zeuzera d'urrillei* H.-Sch. In the forewing, R_{2+3} is quite fused with R_1 above *dc*, so that R_3 appears to be a *second* radial sector arising from R_1. Notice the difference in venation of fore- and hindwings (heteroneurism).

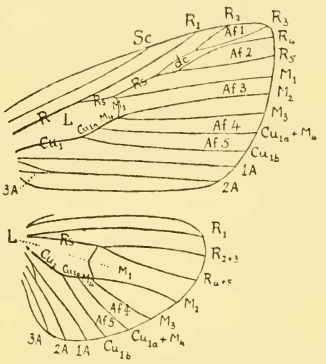
† Wing-venation of *Castnia* sp., (from Sharp). Notice the presence of the archaic Cu_2 in forewing, also the incomplete formation of M at *mf*. An example of heteroneuric venation.

venation" based on the Protomecopterous wing-type, and solved by means of the trigamma-key.

Two of the main objects of this paper are, (*a*) the establishment of the homology of each Lepidopterous vein with a vein of the archaic Protomecopterous wing-type, and hence with a corresponding vein in all other Orders of Insects; (*b*) the establishment of correct homologies between the veins of the fore- and hindwings in Lepidoptera. The former object is illustrated in Text-figs. 1-6. The latter may be shown by drawing up a



Text-fig. 6.*



Text-fig. 7.†

table showing the true homologies of the veins and their designations in fore- and hindwings under (1) the numerical system in use at the present time by British Lepidopterists, and (2) the Staudinger-Schatz notation.

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* Wing-venation of the butterfly *Euploea corinna* Macl., (from Waterhouse and Lyell). The Lepidopterous cell (L) is completely formed in both wings. An example of heteroneuric venation.

† Hampson's diagram of typical Moth-venation (from Sharp). The formation of the radial branches towards apex of forewing has been corrected (in many forms *dc* closes completely up). Heteroneuric venation.

Table of Homologies of the Wing-Veins of Lepidoptera.

Correct Name (Comstock-Needham).	Numerical Notation.		Staudinger-Schatz Notation.	
	Forewing.	Hindwing.	Forewing.	Hindwing.
Costal vein (C)	(in all recent Insects, fused with wing-border)			
Subcostal vein (Sc)	12	(missing)	C	(missing)
Radius (main stem) R_1	11	8	Sc^1	C
Radial Sector, Rs :—				
First branch, R_2	10	7	Sc^2	Sc
Second branch, R_3...	9		Sc^3	
Third branch, R_4	8	6	Sc^4	OR
Fourth branch, R_5...	7		Sc^5	
Media, M :—				
First branch, M_1	6	(missing)	OR	(missing)
Second branch, M_2	5	5	UR	UR
The Trigamma: Third branch, M_3	4	4	M^3	M^3
The Trigamma: Fourth branch, captured by $Cu_{1a} = Cu_{1a} + M_4$				
The Trigamma: First cubitus, Cu_1 :—	3	3	M^2	M^2
The Trigamma: Upper branch (captures M_4) $= Cu_{1a} + M_4$				
The Trigamma: Lower branch, Cu_{1b}	2	2	M^1	M^1
Second cubitus, Cu_2	(often absent, but in *Castnia* 1d)			
First analis, 1A	1*c*	1*c*	SM	SN
Second analis or axillary, 2A	1*b*	1*b*	1A	1A
Third analis or basilar, 3A	1*a*	1*a*	2A	2A

It will be seen that, in the Numerical Notation, the veins numbered from 6 to 11 are falsely homologised in fore- and hind-wings. The same fault is apparent in the Staudinger-Schatz Notation. The author believes that the true scientific spirit will no longer tolerate false homologies in the interpretation of wing-venations, and the systems that perpetuate them must give way to a system of correct homologies. This alone would be sufficient justification for the adoption of a new system. If we add to this, that the system here offered has two other great advantages, viz., (*a*) that it brings the Lepidopterous venation into line with that of all the primitive Orders to which the Comstock-Needham System is readily applied, and (*b*) that, by the use of the *trigamma* as a key, the veriest tyro can unlock the secrets of the Lepidopterous wing with ease, while supposedly aberrant forms like *Castnia* fall simply and readily into their proper places, the case for the adoption of the new system becomes irresistible.

Believing that the question of jugum and frenulum is of less importance than the actual wing-venational scheme, the author proposes to subdivide the Order Lepidoptera into two primary divisions.

A. *Lepidoptera Homoneura*, with venations of fore- and hind-wings closely similar and of primitive design. (This includes *Micropterygidæ* and *Hepialidæ*).

B. *Lepidoptera Heteroneura*, with the venation of the hind-wing reduced, and differing widely from that of the forewing. (This includes all the rest).

Explanation of Notation used in the Text-figures.

All the main veins (C, Sc, R, M, Cu, and A) and their branches, as named in the Table of Homologies on p.172. In addition :—

Closed cells (primary): *dc.*, discoidal or radial cell; *mc.*, median cell. (Secondary) : L., the Lepidopterous "cell."

Junctions or forkings of main veins : *cuf.*, first forking of Cu; *cuf'.*, second forking of Cu (Cu_1); *mf.*, the thyridium, or median forking; *rf.*, first forking of R; *rf'.*, second forking of R (Rs).

The five primary *Apical Forks: Af1* (between R_2 and R_3); *Af2* (between R_4 and R_5); *Af3* (between M_1 and M_2); *Af4* (be-

tween M_3 and M_4); *Af5*, between Cu_{1a} and Cu_{1b}—*pt.* = pterostigma.

Postscript (*added April 16th, 1917*).—Since the above was written, I have carried out an exhaustive study of the Australian Mecoptera (Scorpion-flies) in my collection. These consist of representatives of the families *Bittacidæ*, *Choristidæ*, and a remarkable new family of very small Scorpion-flies, which will be dealt with in a separate paper. As these last are strong-flying insects, in which the wings appear to be connected during flight, I examined their wings for signs of a coupling-apparatus. I found that they all possessed a well-formed basal coupling-apparatus of the type described for the Neuroptera Planipennia, viz., a *jugal lobe* near the base of the forewing posteriorly, and a *jugal process* anteriorly on the base of the costa of the hindwing. From this jugal process there arise *two strong bristles directed obliquely outwards*, so as to constitute a true frenulum, exactly homologous with that found in Planipennia, and in the females of many moths. The same structures are present in *Choristidæ*, but smaller, while their vestiges can be seen even in the *Bittacidæ*.

Since, therefore, the *frenulum* has been shown now to occur normally in *three* Orders, while the *jugum* (as developed in the *Hepialidæ*) is not to be paralleled outside the Order Lepidoptera, it is clear that we must revise our ideas of the relative archaism of the Jugatæ and Frenatæ. The original or ancestral Lepidopteron must have possessed a frenulum derived from an ancestor common to the Lepidoptera, Mecoptera, and Planipennia. On the other hand, the jugum of *Hepialidæ* must have been a very early specialisation developed from the ancestral jugal lobe of the forewing, with complete loss of the original frenulum on the hindwing. The *Micropterygidæ* must have followed a somewhat similar (possibly even earlier) line of specialisation.

The Frenatæ or Heteroneura, then, are the main stem of the Lepidoptera, while the Jugatæ or Homoneura are an archaic side-branch, from which no other existing families of the Order can possibly have been derived. R.J.T.